

Spatial and temporal patterns in larval supply at hydrothermal vents in the northeast Pacific Ocean

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Abstract

Larval supply in marine benthic invertebrates influences patterns of settlement and recruitment to adult populations. To successfully colonize newly formed or distant hydrothermal vents, which are discontinuous and ephemeral habitats, larvae of vent invertebrates must possess long-range dispersal abilities. However, a significant proportion of locally produced larvae must remain within the adult habitat to maintain the observed dense assemblages of invertebrates. I compared spatial and temporal patterns in larval availability (flux and abundance) at hydrothermal vents within and between ridge segments in the northeast Pacific ocean at Axial Seamount and Endeavour Segment on the Juan de Fuca Ridge and at Magic Mountain on Explorer Ridge. Near-bottom (within 50 cm) larval supply (individuals $m^{-2} d^{-1}$) at five vents on Axial Seamount, measured with passively collecting traps in 2000 and 2001, varied temporally by an order of magnitude, but not spatially at scales of tens of meters to kilometers. The most abundant larval taxa were gastropods (particularly the limpet *Lepetodrilus fucensis*) and polychaetes. Larval abundance in the water column within the axial valley was measured with net tows by the remotely operated vehicle ROPOS at the three ridge segments: Axial Seamount (2000, 2001); Endeavour Segment (2001, 2002); Magic Mountain (2002). Abundance was greater by an order of magnitude at the Endeavour Segment than at Axial Seamount and Magic Mountain, and it did not differ between on-vent (within tens of meters) and off-vent (up to 5 km from the venting source) locations within the axial valley. The uniformly high abundance of larvae within axial valleys suggests that larval supply within a ridge segment is most likely localized, implying significant larval retention on the scale of vent fields and possibly ridge segments.

In assemblages of marine benthic invertebrates, larval supply has been tightly linked to larval dispersal or retention (Shanks and Wright 1987; Pineda 1994) and suggested to influence the magnitude of settlement and, in instances of pronounced pulses, recruitment (Gaines et al. 1985; Minchinton and Scheibling 1991). Over large horizontal scales

(10s to 1,000s of kilometers), dispersal is mainly regulated by hydrodynamics because invertebrate larvae are weak swimmers and passively advected by currents (Scheltema 1986; Roughgarden et al. 1988; Metaxas 2001). However, on small vertical scales (<100s of meters) and in areas of reduced flow, such as the benthic boundary layer, larval dispersal is likely influenced by both hydrodynamics and larval behavior (Butman 1987; Metaxas 2001).

The ephemeral nature of these habitats and high endemism implies evolutionary pressure for long-distance larval dispersal by vent organisms for successful colonization of newly formed vent sites. Because vent sites are spatially separated by 100s to 1,000s of kilometers, the proposed mechanisms of between-vent site larval dispersal have used models with point estimates of hydrodynamics and probable duration of larval stages (e.g., Mullineaux and France 1995; Kim and Mullineaux 1998; Marsh et al. 2001). These studies have estimated realistic numbers of larvae that must be advected between vent sites by the dominant flow regime to maintain genetic homogeneity and colonization of new habitats. For example, Chevalloné et al. (1997) estimated that a single migrant per generation exchanged between populations of alvinellid polychaetes was sufficient to maintain genetic mixing among vent sites between 14°N and 7°N on the East Pacific Rise. To be successful, this migrant must travel along axis for 8 days or 8–30 km. For *Riftia pachyptila*, it was estimated that the maximum along-axis distance travelled by larvae 20 days after their release is ~90 km (Marsh et al. 2001).

A conflicting constraint on larval supply at hydrothermal vent habitats implies evolution of mechanisms to enhance larval retention within a vent site. In nonvent ecosystems,

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larval mortality can be as great as 90% during the dispersal phase of life history (Rumrill 1990). Marsh et al. (2001) estimated that 61% of larvae of *R. pachyptila* could be lost during dispersal through advection off the spreading axis to unsuitable habitats. Given the low probability of larval dispersal between active vent sites suggested by existing models, most larvae within a vent site must be produced locally to sustain populations on ecological time scales.

Presently, our understanding of the magnitude of larval retention in hydrothermal vents is limited because only a few studies have measured plankton abundance in the water column overlying these habitats. Although abundance of larvae of vent invertebrates can be elevated inside relative to outside hydrothermal plumes (Mullineaux et al. 1995), it can also be greater near the bottom (within 15 m) than higher in the plume (Kim et al. 1994; Kim and Mullineaux 1998).

I measured larval abundance and potential larval supply at hydrothermal vent sites on the Juan de Fuca (Axial Seamount and Endeavour Segment) and Explorer (Magic Mountain) Ridges (Fig. 1). Specifically, I measured spatial (tens of meters to kilometers) and temporal (annual) variability in larval abundance near the bottom (0.5 m) at five different vents on Axial Seamount. I also obtained an estimate of larval abundance within the axial valley at different heights in the water column overlying vents (5–100 m above bottom), both immediately above as well as at horizontal distances up to several kilometers from the venting source at all three sites. This is the first study to provide measures of the magnitude and spatial variability in larval flux to the benthos at hydrothermal vents. Also, it adds to our limited information on larval abundance in the water column in the immediate vicinity of the venting source, particularly at Axial Seamount and Magic Mountain, where such samples have not been collected to date.

Study sites

Axial Seamount is located on the spreading axis of the Juan de Fuca Ridge (45°56'N, 130°W), and the caldera (3 km × 8 km × 100 m deep) occurs at ~1,550 m depth (Fornari and Embley 1995). It has been suggested that Axial Seamount is the most volcanically active segment of the Juan de Fuca Ridge, with the most recent eruption having occurred in early 1998 (Embley and Baker 1999). It is the location of the New Millennium Observatory, which is a multiyear effort (initiated in 1996) to collect multidisciplinary time series data. Consequently, the macrobenthic assemblages have been studied before and after the eruption (e.g., Tunnicliffe et al. 1985; Marcus and Tunnicliffe 2002; Marcus 2003).

The Endeavour Segment is located ~200 km north of Axial Seamount on the Juan de Fuca Ridge (47°57'N, 129°W) at ~2,200 m depth. It consists of a narrow axial valley (~1 km in width) along a north–south orientation. Hydrothermal venting is vigorous but more temporally stable than at Axial Seamount. Endeavour has been the focus of extensive macrofaunal studies since the 1980s (e.g., Sarrazin et al. 1997; Sarrazin and Juniper 1999; Tsurumi and Tunnicliffe 2003).

Magic Mountain (49°46'N, 130°15'W) is located on Ex-

plorer Ridge at ~1,780 m depth. Only one study has provided a cursory description of the macrobiological assemblages at this site (Tunnicliffe et al. 1986). In 2002, Magic Mountain was revisited, detailed geological maps were generated, and geological, chemical, and biological samples were collected.

Materials and methods

To estimate larval supply (individuals m⁻² d⁻¹) to the benthos at Axial Seamount, four passively collecting larval traps (based on the design by Yund et al. 1991) were deployed at each of Marker 33 and Crack vents in 2000 and at Cloud, ROPOS, and Virgin vents in 2001 with the use of the remotely operated vehicle (ROV) ROPOS. The cylindrical polybutyrate traps were 50 cm high, 6.73 cm in diameter (aspect ratio 7.4, Reynolds number ~3,000), and filled with 10% buffered formalin. Preliminary studies with dye in the field indicated that eddy penetration did not exceed 7 cm. The traps were deployed capped with a rubber stopper, positioned ~1 m from one another and 1–5 m from the vent opening (to prevent negative effects of a possible spill on the vent assemblage), and uncapped. After 7–10 days, the traps were capped and retrieved, and the samples were concentrated through a 63- μ m mesh sieve and later enumerated under a stereomicroscope. Two of the four traps deployed at Cloud vent were accidentally tipped over during regular operations and are not included in the analysis.

Plankton samples were collected in the water column immediately above, as well as at distances of 100s of meters to kilometers (but within the axial valley) from venting sources at Axial Seamount, Endeavour Segment, and Magic Mountain in 2000, 2001, and 2002, with net (63- μ m mesh) tows done by the ROV ROPOS (Fig. 1; Table 1). In 2000 and 2001, the net was held with a manipulator arm below the ROV while towing, whereas in 2002, the net was mounted on the bumper bar on the top front side of the ROV. The nets remained closed until the beginning and were cinched at the end of each tow to prevent inadvertent collection or loss of samples. On board ship, the contents of the net were gently rinsed down into the cod end and the sample was preserved in 80% (in 2000 and 2001) or 95% (in 2002) ethanol; the larvae were enumerated later in the entire sample under a stereomicroscope. Sample volumes of the net samples were calculated as $\pi r^2 ut$, where r is the radius of the net mouth opening (=0.15 m), u is the speed of the ROV during the tow (ranging from 0.5 to 1 knot), and t is the total time period of the tow.

Larvae were identified to the lowest taxonomic level possible on the basis of morphology. Among the gastropods, I identified a single vent limpet morph, which I assigned to *Lepetodrilus fucensis*, on the basis of the protoconch shape of identifiable juveniles and the numerical dominance of juveniles and adults of this species at the Juan de Fuca vents. Although it is possible that other species were present and misidentified, they would have constituted <1% of total abundance. Similarly, I identified a single vent snail morph, which I assigned to *Depressigyra globulus*. However, this category might include some individuals belonging to *Pro-*

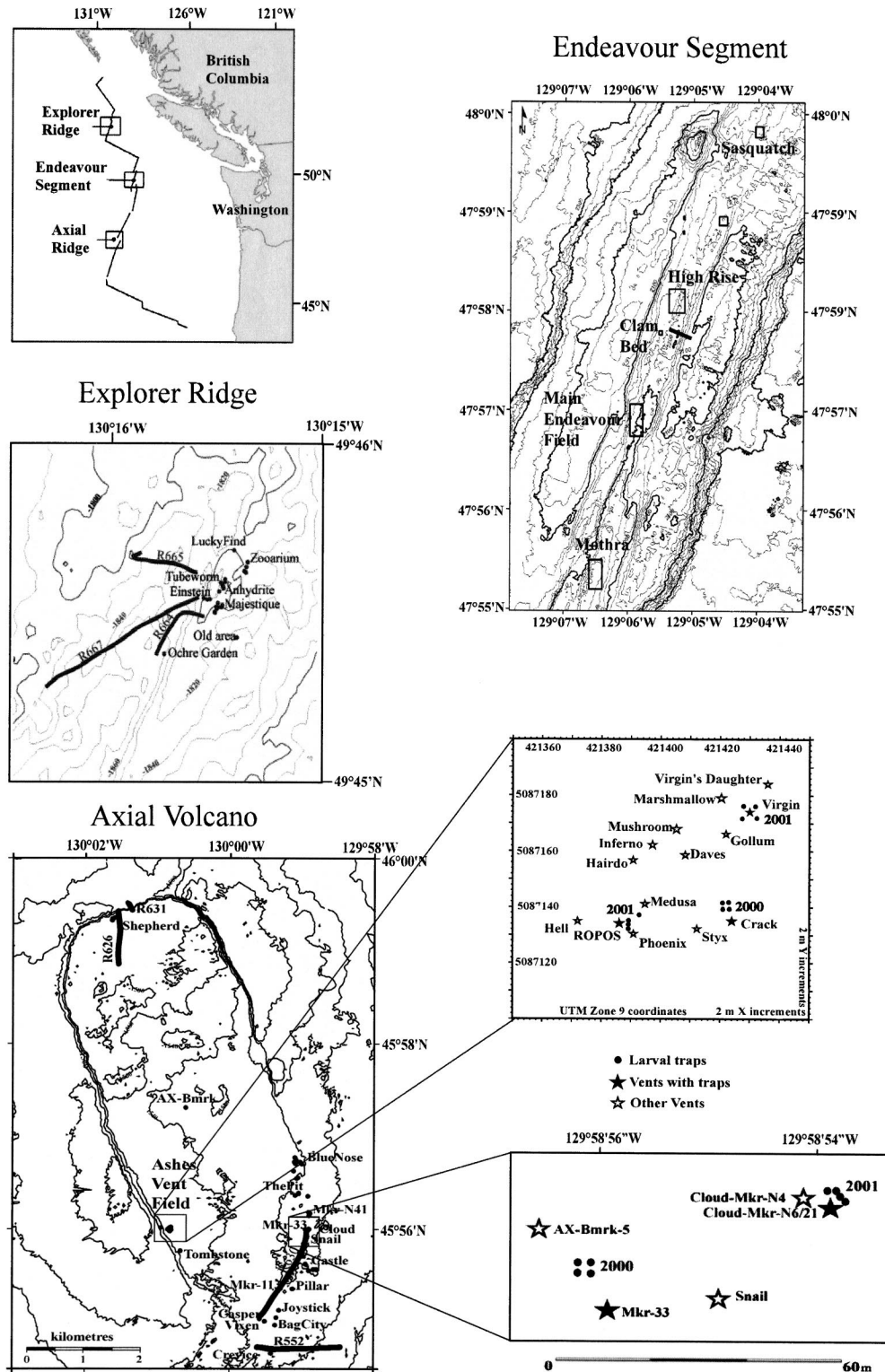


Fig. 1. Location map of Axial Seamount, Endeavour Segment, and Magic Mountain on Juan de Fuca and Explorer Ridges. Transects of net tows done at all three sites are shown as black lines in higher resolution maps of each segment. The ROPOS dive number for each tow is given above the line (see Table 1 for year and volume of each tow). Insets show locations of passively collecting larval traps in the caldera of Axial Volcano in 2000 and 2001.

Table 1. Sampling characteristics of net tows by the remotely operated vehicle ROPOS at ridge segments in the northeast Pacific in 2000, 2001, and 2002.

Site	Year	Location	Dive	Height above bottom (m)	Volume (m ³)
Axial Seamount	2000	South Pillow Mound (off-vent)	R546	25	1,986
		South of Bag City (off-vent)	R552	15	684
	2001	CASM (off-vent)	R626	25	816
		Marker 33 to Caspar vent (off-vent)	R630	70–80	304
		Wall of northern caldera (off-vent)	R631	50–100	87
Endeavour Segment	2001	East of Clam Bed (off-vent)	R593	15–25	33
	2002	Clam Bed (on-vent)	R682	20	33
		Main Endeavour Field (Bastille vent) (on-vent)	R683	20	33
		Main Endeavour Field (on-vent)	R685	2–20	52
Magic Mountain	2002	Tubworm Chimney (on-vent)	R666	5	68
		Einstein (on-vent)	R668	5	66
		Majestique (on-vent)	R669	5	66
		Zooarium (on-vent)	R670	7	68
		South of Magic Mountain (off-vent)	R664	20	55
		West of Magic Mountain (off-vent)	R665	2–5	34
		Across rift valley/Southern Explorer Ridge (off-vent)	R667	20	76

vanna variabilis (<5% of total). Larvae of pelagic gastropods included mainly heteropods and a few (10%) thecosomes. Polychaete larvae were present in all developmental stages (trochophores, metatrochophores, and nectochaetes), but the assignment of polychaete individuals in these early life history stages to genus or species is problematic. The nectochaetes included four identified families in approximately equal relative abundance: phyllodocids, hesionids, dorvilleids, and ampharetids. Most bivalves were in the D-stage and could not be identified to order. The few veligers present were assigned to the order Veneroidea and most likely belonged to the genus *Calypptogena*. A few other taxa, although present sporadically, were assigned to class because of their distinct morphology, more advanced stage, or both.

Results

Larval supply to the benthos at Axial Seamount measured with passive larval traps varied temporally but not spatially at scales of tens of meters to 2 km (Fig. 2). The most abundant taxa were gastropod larvae and larval polychaetes. Bivalves were extremely abundant only at ROPOS vent in 2001. There was approximately an order of magnitude difference in flux of the most abundant taxa between 2000 and 2001. However, within each year, there was no significant difference between sites for any taxon tested (2000: in all cases, $t_{\text{calc}} < t_{0.05/2(6)} = 2.44$; 2001: $F_{\text{calc}} < F_{1-0.05,2,7} = 4.74$).

At Axial Seamount, gastropods and polychaetes also showed great larval abundance in the plankton within the axial valley relative to other taxa, as in the larval traps (Fig. 3). Copepod nauplii also were abundant in the net tows. Some groups, such as gastropods other than limpets and bivalves, were only present in 1 of the 2 yr. Despite the ap-

proximate order of magnitude difference in limpet abundance between 2000 and 2001, there was no significant difference between years in the abundance of any group that was present in both years (in all cases, $t_{\text{calc}} < t_{0.05/2(3)} = 3.18$).

Larval abundance in the plankton was greater at Endeavour than the other two ridge segments (Fig. 3). The most abundant taxa were gastropods, but a few polychaete larvae were also collected. Abundance was similar between tows done on- and off-vent, although sampled at different years.

Larval abundance in the plankton at Magic Mountain on Explorer Ridge was intermediate in magnitude between that at Axial Seamount and Endeavour and did not vary significantly between on- and off-vent tows (in all cases, $t_{\text{calc}} < t_{0.05/2(5)} = 2.57$) (Fig. 3). Unlike the other two study sites, limpet larvae were not the dominant benthic taxon in the plankton at Magic Mountain.

Larvae and juveniles of other taxa, such as echinoderms and brachyuran zoeae, were also collected at all three sites but were present in low abundance and in few tows per site (Table 2).

Discussion

Larval supply at Axial Seamount, as measured with passive collectors, did not vary spatially at scales of kilometers, particularly for *L. fucensis* and polychaetes, suggesting the presence of a homogeneous larval pool across the floor of the caldera. This homogeneity is particularly striking because adult faunal density and composition varies greatly among the vents where larval flux was measured. Most mature vents (e.g., Cloud, Marker 33, ROPOS) harbor lush assemblages (~100% cover), with the most abundant taxa being the vestimentiferan *Ridgeia piscesae*, the gastropods *L.*

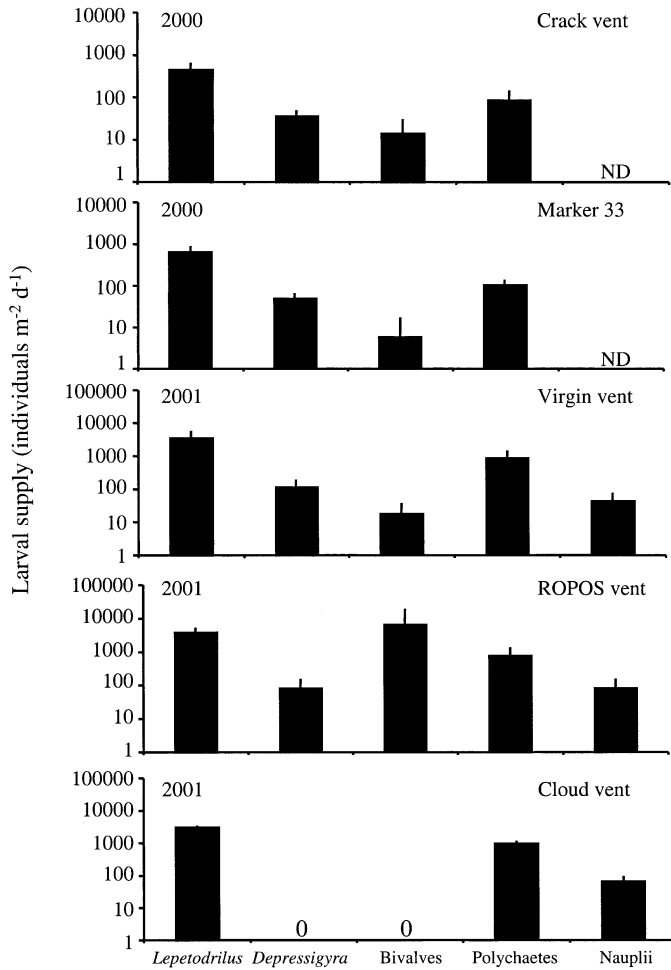


Fig. 2. Larval supply of benthic invertebrates as measured with passive collectors at five vents on Axial Seamount in 2000 and 2001. Nauplii belonged to Calanoida and Harpacticoida. Error bars are standard deviations ($n = 4$, except at Cloud vent, where $n = 2$). ND, not determined.

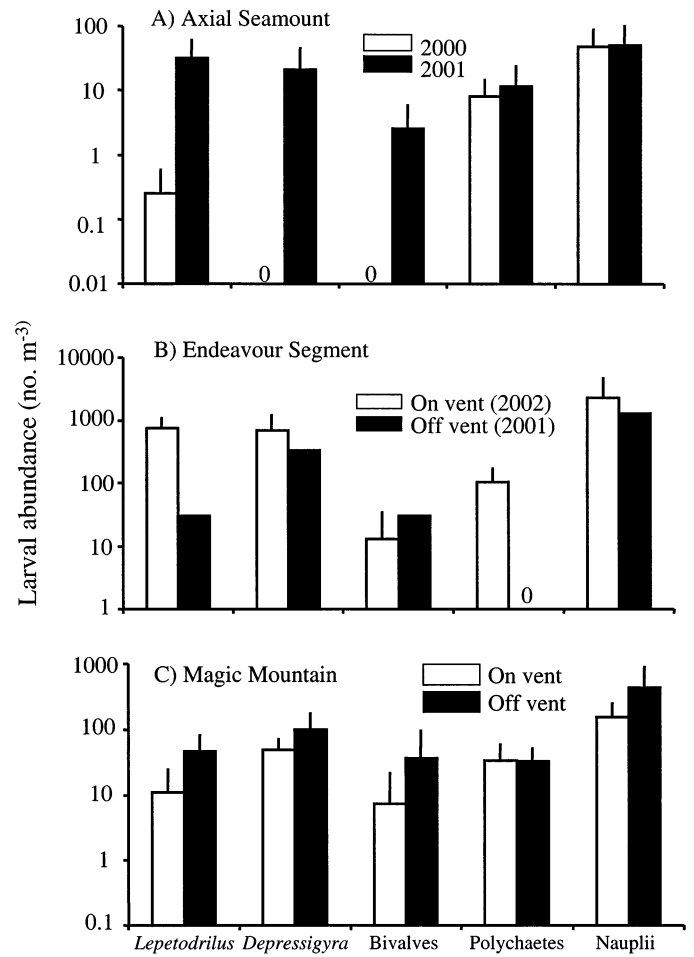


Fig. 3. Larval abundance from net tows within the axial valley (A) at distances of more than tens of meters from a venting source at Axial Seamount in 2000 and 2001 (2000: $n = 2$; 2001: $n = 3$); (B) at distances <100 s of meters (on-vent) and >100 s of meters (off-vent) from a venting source at Endeavour Segment in 2001 and 2002 ($n = 3$); (C) at distances <100 s of meters (on-vent) and >100 s of meters (off-vent) from a venting source at Magic Mountain on Explorer Ridge in 2002 (on-vent: $n = 4$; off-vent: $n = 3$). Error bars are standard deviations.

Table 2. Sporadically collected taxa in net tows by the remotely operated vehicle ROPOS at Axial Seamount, Endeavour Segment, and Explorer Ridge in 2000, 2001, and 2002.

Location	Year	Taxon	Abundance (mean \pm SD (n) no. m^{-3})
Axial Seamount, off-vent	2000 2001	Brachyuran zoeae	$1.01 \pm 1.42(2)$
		Siboglinid juveniles	$3.90 \pm 5.38(3)$
		Ceratulid nectochaetes	$2.19 \pm 3.80(3)$
		Asteroid juveniles	$0.41 \pm 0.71(3)$
		Scyphozoan ephyrae	$1.10 \pm 1.90(3)$
		Brachyuran zoeae	$1.10 \pm 1.90(3)$
Endeavour, on-vent	2002	Echinoplutei (2-arm)	$6.41 \pm 11.10(3)$
		Heteropods	$120.2 \pm 160.9(2)$
Explorer, off-vent	2002	Ophiuroid juveniles	$4.39 \pm 7.60(3)$

fucensis and *D. globulus*, and the polychaetes *Paralvinella pandorae*, *Paralvinella palmiformis*, and *Amphisamytha galapagensis* (Marcus and Tunnicliffe 2002; Marcus 2003; Tsurumi and Tunnicliffe 2003; pers. obs.). However, the relative abundance of each taxon can vary between vents. For example in 2000, *L. fucensis* was relatively more abundant at Marker 33 than at Cloud vent, whereas the opposite trend was observed for *P. palmiformis* (Marcus 2003). Interestingly, Virgin vent is a structurally unstable anhydrite mound, continuously collapsing and reforming through dissolution and precipitation on daily to weekly scales. Consequently, the assemblages at this vent consist of sparsely populated assemblages of polychaetes at the base of the mound (pers. obs.). This study suggests that this pattern might result from limited availability of physical substrate rather than potential settlers.

Larval supply of the numerically dominant *L. fucensis* and polychaetes at Axial Volcano varied interannually by approximately an order of magnitude. Adult assemblages can also vary markedly over time, as ecological succession unfolds after an eruption (Marcus 2003). For example, the relative abundance of *L. fucensis* increased fivefold between 2000 and 2001 at Cloud vent (Marcus 2003). Interestingly, pulses in supply can occur at small (meters) spatial scales, as evidenced by the large abundance of bivalves in the traps at ROPOS in 2001. In 2002, juvenile bivalves were collected only on settlement substrates deployed at ROPOS the previous year (Kelly and Metaxas unpubl. data), suggesting that such pulses in larval supply might result in spatially heterogeneous patterns in recruitment.

Several studies have addressed potential limitations of passive collectors used to assess particle flux in the laboratory and the field (e.g., Hargrave and Burns 1979; Butman et al. 1986; Yund et al. 1991). On the basis of these studies, the design of the larval traps used in my study fulfilled several requirements, and collection efficiency (although not measured) should approach 100% in the vent environment of low horizontal flow speeds. Given the aspect ratio and diameter of the traps, it is unlikely both that larvae were undercollected and that overcollection exceeded half an order of magnitude. Thus, I believe that both the general patterns and the order of magnitude of the estimates in larval supply that I measured are realistic. Unfortunately, sampling constraints did not allow me to resolve temporal patterns in larval supply at subannual scales.

Larval abundance of vent taxa in the plankton also reflected the composition of adult assemblages at all vent sites. At Axial Seamount, the most abundant larval taxa in the plankton were gastropods and polychaetes, as in the adult assemblages over the same period (Marcus 2003; Tsurumi and Tunnicliffe 2003). The abundance of larval vent gastropods in the plankton was much greater in 2001 than 2000, most likely reflecting successional patterns observed in the adult assemblages, where the relative abundance of gastropods increases with age of the assemblage (Marcus 2003). I collected echinoderms near CASM and brachyuran larvae near Bag City and South Pillow Mound (Fig. 1). Tunnicliffe et al. (1986) indicated that, among the nonvent fauna, echinoderms and sponges were abundant near the northern end, whereas brachyuran crabs and macrourid fish were observed near the southern end of the caldera.

At Endeavour and Explorer, the dominant larval taxa also were gastropods and polychaetes. Although the composition of adult assemblages at Endeavour was not described during this study, Sarrazin et al. (1997) documented the same numerically dominant species at Main Endeavour Field as Marcus (2003) at Axial Seamount. At Magic Mountain, Tunnicliffe et al. (1986) recorded high variability in faunal composition among vent edifices. The dominant fauna were vestimentiferans, the polychaetes *Paralvinella* sp. and *A. galapagensis*, and the gastropods limpet sp. 1 and trochid snails.

Within the axial valley at Axial Seamount and Magic Mountain, larval abundance in the water column was similar to that observed by Kim et al. (1994) at hydrothermal vents at 9°50'N along the East Pacific Rise (also at 20–25 m above the bottom), but it was greater by an order of magnitude at the Endeavour Segment. It is possible that this between-segment difference reflects a difference in the density of the adult assemblages and, consequently, in locally produced larvae. For example, the assemblages at Explorer are not as dense or extensive as at the other two sites (Tunnicliffe et al. 1986; pers. obs.), and the 1998 eruption at Axial Volcano resulted in a short-term decrease in adult densities (Marcus 2003). Unfortunately, there are no quantitative descriptions of the adult assemblages at all three study sites, and such comparisons are not possible.

Larval abundance in the plankton did not differ between on-vent (within tens of meters) and off-vent (up to tens of kilometers from the venting source) locations. Although the polychaete larvae were not identified to species and might have originated in nonvent habitats, the gastropod larvae were of vent origin. As with larval flux, these patterns in larval abundance in the plankton also support the presence of a homogeneous larval pool of vent fauna within the axial valley. Most likely, this pool becomes more dilute with increasing distance from the valley, particularly if vent larvae are being transported within the hydrothermal plume, as suggested by Mullineaux and France (1995).

Given the observed concentrations of larvae, it is most likely that this homogeneous pool is generated by larvae produced locally rather than advected from other ridge segments. The hydrographic conditions both at Axial Volcano and Endeavour (not quantified at Magic Mountain) are conducive to larval retention within the caldera and axial valley, respectively. The direction of mean circulation at the summit of the volcano (10s to 100s of meters above the floor of the caldera) is anticyclonic (Lavelle et al. 2003) and flow speeds range between 0.7 cm s⁻¹ and 18 cm s⁻¹, with mean values of ~7 cm s⁻¹ (Baker et al. 1990; Cannon and Pashinski 1990; Lavelle et al. 2001). Turbidity measures indicate that although most hydrothermal venting occurs at the southeastern region of the caldera, the hydrothermal plume appears to be trapped immediately above the volcano (Lavelle et al. 2003). At Endeavour, a steady along-axis background flow is superimposed by cross-axis zero-mean oscillatory currents with mean velocities of 10 cm s⁻¹ (Thompson et al. 2003). Within the valley, the oscillatory currents are suppressed and background flow is 2–3 cm s⁻¹, and above the ridge crest (>75–100 m above bottom), the along-axis background flow is to the southwest (Thompson et al. 2003).

Plume-induced flow draws an “inflow” of cold water within the valley below 75 m above bottom to the northeast, likely facilitating larval retention (Thompson et al. 2003).

Interestingly, the magnitude in larval flux I measured for different taxa at vents is also of the same order of magnitude as for related taxa in coastal systems, as measured by a comparable trap design (Butman 1989; Yund et al. 1991). Given the high biomass and concentration of invertebrates at vents, it is not surprising that larval supply to the bottom can be as high as in coastal systems.

The uniformity in larval flux to the benthos at several vent sites within a ridge segment and in larval abundance in the plankton within the axial valley at different distances from the venting source suggest larval retention. Retention would most likely be facilitated by local hydrodynamics but might also involve certain larval behavioral adaptations. More detailed studies of hydrodynamics in the benthic boundary layer, in combination with particle releases, are needed to evaluate the magnitude and assess mechanisms of larval retention at hydrothermal vents.

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